MATING BEHAVIOR OF *ACIURINA MEXICANA* (ACZÉL) (DIPTERA: TEPHRITIDAE)

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Abstract. —Observations on the mating behavior of *Aciurina mexicana* (Aczél) in the laboratory are presented. Courtship and agonistic displays are named and described in detail. These displays include stereotypic body postures and wing movements, nuptial feeding, and abdominal inflation with odor production by males. Preliminary observations suggest that the male's nuptial gift is produced from the crop, and the source of the male odor is the abdominal pleura. Mating behavior of *A. mexicana* is compared with other *Aciurina* species and tephritid flies generally. Potential use of mating behavior in fruit fly systematics is noted.

Key Words: Tephritidae, *Aciurina*, mating behavior, sexual displays, nuptial gift, pheromone, systematics

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At least 12 species of *Aciurina* occur in the western United States and northern Mexico (Steyskal 1984, Dodson and George 1986). Larvae of the species for which host plants are known form galls on asteraceous plants, primarily *Chrysothamnus* species (Steyskal 1984, Dodson 1987b).

Mating behavior has been observed for a number of *Aciurina* species. Tauber and Tauber (1967) reported the reproductive behavior and biology of *Aciurina ferruginea* (Doane) from California. Wangberg (1981) commented on the mating behavior of *A. ferruginea, A. maculata* (Cole), *A. semilucida* (Bates), *A. trixa* Curran, and an undescribed species (probably *A. idahoensis* Steyskal—see Steyskal [1984]) from Idaho. Dodson (1987b) described the mating behavior of *A. trixa* in New Mexico.

Dodson (1987b) predicted that most species of *Aciurina* would exhibit a similar mating strategy which he termed the "male-searching mating system." In this system,

males move about the host plant scanning for conspecifics and attempt to copulate with any females encountered. Evidently, courtship is limited to a few brief wing displays and may not precede attempts at copulation. Successful mating is dependent more on a male's ability to maintain a mounted position on a female (Dodson pers. comm.).

Aciurina mexicana (Aczél) occurs in southern Arizona, southern California, and northern Mexico where larvae form stem galls on *Baccharis sarothroides* Gray (Steyskal 1984). Contrary to what has been reported for other *Aciurina* species, precopulatory behavior in *A. mexicana* is protracted and involves a number of complex sexual displays. This paper describes the mating behavior of *A. mexicana*.

MATERIALS AND METHODS

Specimens used in this study were swept from *B. sarothroides* located 14.3 km SE of Continental, Ariz. (Pima Co.) on 16 Feb.

and 1 Mar. 1986. Flies were separated by sex and caged, one to several, in 0.3–1 clear plastic cups. Cages were fitted with a cotton wick for water and ventilated by a series of small punctures around the top and bottom. Flies were fed a diet of honey containing a small quantity of nutritional yeast. The honey/yeast mixture was provided *ad lib* on a paper strip suspended in the cage; water was supplied twice daily by saturating the cotton wick. Flies were kept in the laboratory at ambient temperature, relative humidity, and photoperiod.

Observations of mating behavior began by placing a pair of flies in a 100×15 mm plastic petri dish. Trial length varied with the flies' activities. Trials were discontinued when one or both flies became unresponsive or agonistic. When copulation occurred, the pair was observed at least until they uncoupled. Petri dishes were changed between trials. Observations were made between 1025 and 1627 hours (MST) on nine dates between 25 Feb. and 10 Mar. 1986. Duration of mating activities was recorded to the nearest minute. Video recordings were used to help analyze behaviors.

Results

Courtship and agonistic displays. — Several displays were typical of one or both sexes of *A. mexicana* during courtship and agonistic interactions. To facilitate discussion, these displays are named and described below. Rotation of the wing refers to twisting the wing so its ventral surface is brought into an anteriorly directed position and the costal margin is pointing upward (Fig. 1). Rotating the wing 90° results in the wing blade being more or less perpendicular to the substrate. Angular measurements of wing movements are visual approximations.

Slow signal: One wing is brought slowly forward to an angle of ca. 90° to the long axis of the body (Fig. 2). As the wing is moved forward the wing blade is rotated ca. 90°. The forward movement of the wing may

be smooth or by intermittent jerks accompanied by slight rotational adjustments. The wing is then slowly returned to its original position and the other wing brought forward in a similar manner. Both sexes exhibited this display.

Wing fanning: Both wings are held outstretched at an angle of ca. 45° to the long axis of the body, with the wing blades rotated between ca. 45° and 90° (Fig. 3). Both wings are then brought forward and returned in short, very rapid, coupled strokes. Bouts of wing fanning were brief (ca. 1 s or less) and sometimes occurred in rapid succession. Only males exhibited this behavior.

Wing flicking: Both wings are held outstretched at an angle of ca. 45° to the long axis of the body, with the wing blades rotated ca. 90° (Fig. 4). Both wings are then brought forward and returned in short, quick strokes, with a brief pause between strokes. Only courting males used this display.

Wing thrust: Both wings are simultaneously and quickly brought forward to an angle of ca. 90° to the long axis of the body; wings are rotated ca. 90° as they are brought forward (Fig. 5). Wings are held in this position as the fly charges toward an intruder. Wing thrusts may be accompanied by waving the forelegs in an aggressive manner ("sparring"), with or without making contact. Wing thrusts and sparring were observed for both sexes.

Wing waving: Wings are alternately brought forward to an angle of ca. 90° to the long axis of the body; the wing is rotated ca. 90° as it is brought forward (Fig. 6). Each wing is returned to its initial position over the back of the fly as the other wing is brought forward. Wing waving is similar to the slow signal, but the wings are brought forward and returned in rapid succession. Wing waving was the basic component of female courtship.

Abdominal inflation: The abdominal pleura of males become swollen during courtship and agonistic intrasexual dis-
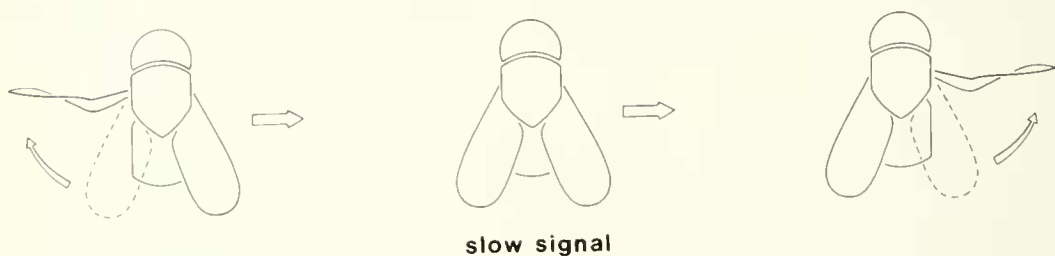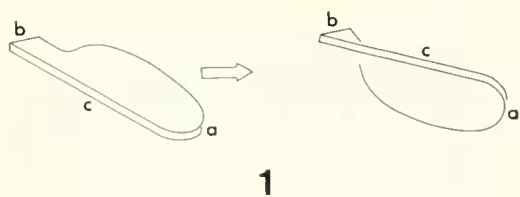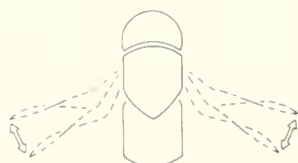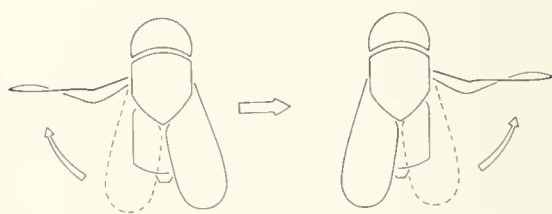
Figs. 1–6. 1. Wing rotation in *Aciurina mexicana* (left anterolateral view). The wing blade goes from parallel to the substrate to perpendicular to the substrate (rotation = 90°). a, wing apex; b, wing base; c, costal margin. Figs. 2–6. Wing displays in *Aciurina mexicana* (dorsal view). 2, Slow signal. 3, Wing fanning. 4, Wing flicking. 5, Wing thrust. 6, Wing waving. See text.

plays. Inflation of the pleura is accompanied by the release of an odor, presumably a pheromone, that is easily detectable by humans.

Nuptial gift: During courtship males produce a clear fluid from their mouthparts and dab it onto the substrate with their labellum. Females are attracted to and feed on the fluid while males attempt mounting. The fluid becomes sticky as it dries. Nuptial gifts that were not entirely consumed were readily eaten by both sexes.

Mating behavior.—A total of 33 trials were conducted and 20.9 h of observations recorded. Courtship displays were observed for either one or both sexes during 26 trials: only males displayed in 11 trials, only females displayed in two trials, and both sexes displayed during 13 trials. No courtship was observed during seven trials. Copulation (n = 7) occurred only in trials where both sexes exhibited courtship displays. Males initiated courtship in 19 trials with two of these resulting in copulation; females initiated in three trials, one resulted in copulation; both flies began courting simultaneously during four trials, all resulted in copulation. Trials in which courtship did not lead to copulation (n = 19) were discontinued when one or both flies were unresponsive (n = 5) or agonistic (n = 14).

After being placed in a petri dish, flies walked about randomly, often with their wings outstretched, or groomed until one or both became cognizant of the other. Both sexes rhythmically extended and retracted their mouth parts during mating as well as nonmating activities. Courtship and mating were not limited to a particular surface within the dish.

The most typical and complete sequence of mating behaviors from courtship through copulation is given below. Deviations from this pattern are then discussed.

The body of males during noncourtship activities was held close to the substrate. During courtship, however, males extended

their legs and held their bodies well above the substrate. In this raised posture males rocked from side to side and displayed wing flicking and abdominal inflation (n = 24). While displaying, males remained stationary or moved forward by short, uncoupled steps. Males typically approached females from the front. When within a few centimeters of the female, the male turned, moved a short distance away, turned back to face the female, and reapproached. This sequence was repeated several times prior to producing a nuptial gift.

Females responded to courting males by wing waving (n = 13). The intensity of wing waving was affected by the male's proximity. As the male moved away from the female, wing waving was less vigorous or ceased; as he reapproached, wing waving became more vigorous or was resumed.

After a period of reciprocal displays, the male, while continuing to display, became stationary and produced a nuptial gift (n = 7). Although males usually continued to court females that became unresponsive (n = 2) or agonistic (n = 4), nuptial gifts were produced only after vigorous wing waving by females. While continuing her wing waving, the female approached the male and began to feed on the nuptial gift. As the female fed, her wing waving became very rapid. Males displayed for a mean of 8.7 min (n = 7, median = 9 min, range = 2–17 min) before producing a nuptial gift. One male placed his gift on the side of the petri dish, three males placed their gifts on the dish bottom, and three placed a gift on the dish lid.

The male ceased displaying soon after the female began feeding on the nuptial gift. He then retreated a short distance and reapproached the female to attempt mounting. As the male moved away the female ceased to display but continued feeding. As he reapproached the female, his body was close to the substrate and his wings were folded tightly over his abdomen. Males usually

mounted from the side or rear by simply grabbing the female, or by pushing their head under one of the female's wings and climbing upon her abdomen. Females usually continued feeding and remained stationary while the male attempted to mount.

Males probed the tip of the female's oviscape with their surstyli after mounting. Prior to intromission the male grasped the female tightly by hooking his foretarsal claws over the anterolateral margin of her syntergum 1+2; his meso- and metatarsi remained on the substrate. The male maintained a grip on the female's syntergum after intromission; his mesotarsi were held loosely about her fifth or sixth tergum, and his metatarsi were held loosely about her oviscape or trailing behind, touching the substrate or not. The male's abdomen returned to its precourtship size after mounting.

After coupling (n = 7), a pair usually moved a short distance before becoming stationary and usually remained in one place if undisturbed. The male's wings were held over his abdomen during copulation; the female's wings were spread to accommodate his body. Copulation lasted a mean of 1.5 h (n = 6, range = 1.1–1.9 h). (Mean duration of copulation does not include one pair that became uncoupled when inadvertently disturbed.) Males remained motionless during copulation except for adjusting their posture when disturbed by intermittent grooming by the female. Females also were seen to slow signal during copulation.

Uncoupling was brief and seemingly without difficulty. Both sexes spent a short period grooming themselves after uncoupling. Males usually reinitiated courtship, but females either were unresponsive or actively rejected them. No male was seen to remount a female following copulation.

Several deviations from the pattern of courtship described above were observed. Males did not produce a nuptial gift in two of the seven trials that resulted in copulation. Duration of copulation for these two pairs was 1.4 and 1.5 h. During two trials

where gifts were produced and the males were unsuccessful in their first attempts to mount, they reinitiated wing flicking and added more fluid to the gifts. One male added to the gift twice, the other six times; copulation followed in each case. In two other trials the female elicited and fed on a nuptial gift, but then vigorously evaded attempts by the male to mount. In four trials, males showing limited or no displays attempted to mount females; none of these resulted in copulation. During two trials females exhibited wing waving without previous courting by males. In one of these trials the male was unresponsive; in the other, the male attempted mounting and then exhibited agonistic behavior (wing thrusts) during the remainder of the trial (ca. 6 min).

Agonistic behavior. — Wing thrusts were used in an aggressive manner at close distances, inter- or intrasexually. Wing thrusts or sparring, or both, were often used by females to reject courting males (n = 11). Wing fanning accompanied by abdominal inflation and odor production was commonly observed between males in the same container. Wing fanning was observed between a male and female only once.

Females evaded a male's attempt to mount by simply walking or running away. While moving away, females sometimes held or flicked their wings over their abdomen. Females prevented mounted males from copulating by either kicking with their hind legs or pushing the tip of their oviscape to the substrate, or both. Females did this while stationary or while dragging the male.

DISCUSSION

Courtship and agonistic displays. — *A. mexicana* appears to share a number of wing displays with other *Aciurina* species as well as other fruit flies in general. Tauber and Tauber (1967) described wing movements of *A. ferruginea* that are similar to the slow signal of *A. mexicana*. They suggested that the display functioned in intraspecific recognition, courtship, and copulation. This

display also was reported for *A. ferruginea* by Wangberg (1981). Dodson (1987b) described similar wing movements for *A. trixa*. The slow signal of *A. mexicana* occurred when flies were together or alone and could not be associated with any specific activity. Slow signals were often seen while flies, regardless of sex, faced each other at a short distance. This suggests that slow signals may in part operate in conspecific recognition. A similar display occurs in a number of fruit flies (e.g. Nation 1972, Piper 1976, Cavender and Goeden 1982, 1984).

Displays like wing fanning and wing flicking may also occur in *A. bigeloviae* (Cockerell) and *A. trixa* (G. Dodson pers. comm.). "Rowing" of the wings described for *A. trixa* (Dodson 1987b) is similar to wing fanning and wing flicking described here (G. Dodson pers. comm.).

Wing fanning by *A. mexicana* may help direct male odor toward intruders. Dispersal of a sex pheromone by a similar behavior has been suggested for *Anastrepha suspensa* (Loew) and *Ceratitis capitata* (Wiedemann) (Nation 1972, Prokopy and Hendrichs 1979). Alternatively, Sivinski et al. (1984) convincingly demonstrated that wing fanning by males of *A. suspensa* produces sounds that are sexually important, intraspecific signals. No sound was noted during wing fanning by *Aciurina mexicana.*

Wing flicking also may help to disperse and direct male odor. Prior to and intermittently during courtship, males rubbed their hind legs against their abdominal pleura and in turn rubbed their wings. This may transfer odor from the pleura to the wings where it then could be dispersed by wing flicking. The activity may be coincidental with grooming. Male *Anastrepha suspensa* exhibit a similar behavior, and Nation (1972) noted that "this cleaning behavior may spread a sex attractant over the body and wings and provide a greater surface from which it can evaporate." Piper (1976) suggested that wing movements in general may help direct pheromones toward either sex.

Copulating males of *Aciurina ferruginea* may "flick" their wings at approaching males (Tauber and Tauber 1967). In the context of agonistic behavior, this display is similar to the wing thrusts of *A. mexicana.* Sparring, but not wing thrusts, has been reported for *A. trixa* (as "grappling," Dodson [1987b]). A display resembling wing thrusts also has been reported for *Trupanea bisetosa* (Coquillett) and *Paracantha cultaris* (Coquillett) (Cavender and Goeden 1982, 1984). In these flies, however, the display functions in courtship.

Wing displays comparable to wing waving have been reported for *A. ferruginea* and *A. trixa* (Tauber and Tauber 1967, Dodson 1987b) as well as other fruit flies (e.g. Tauber and Toschi 1965, Cavender and Goeden 1982, Dodson 1987b). Dodson (1987b) observed 11 virgin female *A. trixa* to mate after frequently waving their wings ("advertising behavior"). Conversely, none of nine once-mated females exhibited the display (Dodson 1987b). Tauber and Toschi (1965) reported that during the courtship of *Euleia fratria* (Loew), the frequency of "wing waving" and displacement of the wings are indicative of the level of sexual excitation of females. As noted above, frequency and duration of wing waving by *A. mexicana* females was affected by the proximity of a courting male, and males produced nuptial gifts only in the presence of a displaying female.

Although fruit fly wing movements usually are discussed in terms of intraspecific displays, there also is strong evidence for an interspecific role. It was recently shown that wing movement and wing pattern of *Rhagoletis zephyria* Snow and *Zonosemata vittigera* (Coquillett) are important in deterring predation by mimicking the flies' salticid spider predators (Mather and Roitberg 1987, Greene et al. 1987). Further, these authors suggested that spider mimicry may be widespread in the Tephritidae.

Abdominal inflation and odor production have not been reported for other *Aci-*

urina species. Tauber and Tauber (1967) refer to "pumping of the abdomen" in male homosexual encounters of *A. ferruginea,* but it is unclear whether this represents abdominal inflation as discussed here. Abdominal inflation accompanied by odor production has been observed in males of the fruit flies *Dirioxa* (= *Rioxa*) *pornia* (Walker), *Anastrepha ludens* (Loew), *A. suspensa, Trupanea bisetosa,* and *Toxotrypana curvicauda* Gerstäcker (Pritchard 1967, Nation 1972, Cavender and Goeden 1982, Landolt et al. 1985, Robacker and Hart 1985b). Appearance of the inflated pleura of *Aciurina mexicana* was quite similar to that illustrated for *T. bisetosa* (Cavender and Goeden 1982, Fig. 2).

Glandular epidermal cells have been identified in the pleura of abdominal segments 3, 4, and 5 of males of *D. pornia* (Pritchard 1967), seven *Anastrepha* species, and two *Ceratitis* species (Nation 1981). The cells are sex-specific, occurring as a thick band in male pleura; female pleural epidermis is uniformly thin and undifferentiated (Pritchard 1967, Nation 1981). These glandular cells are, at least in part, the probable source of male odor in *D. pornia, A. suspensa,* and *A. ludens* (see Pritchard 1967, Nation 1974, 1981; Robacker and Hart 1985a). Pleura removed from male *Aciurina mexicana* were visibly thicker than those removed from females when compared under a dissecting microscope, regardless of the size of the fly. Based on the above observations, and because odor was detectable only when the pleura were distended, it is likely that the pleura of male *A. mexicana* contain glandular cells that are associated with the male odor.

Odors produced by male *D. pornia, Anastrepha suspensa, A. ludens,* and *Toxotrypana curvicauda* are attractive to females (Pritchard 1967, Nation 1983, Landolt et al. 1985, Robacker and Hart 1985a). The odor produced by *Trupanea bisetosa* is presumably also a sex pheromone (Cavender and Goeden 1982). Courting males of *Aci-*

urina mexicana always produced odor, but it was not shown that the odor was attractive to females. Because male odor was produced during wing fanning, it may also function intrasexually.

The male odor of *A. mexicana* is distinctive, but difficult to describe precisely. The male odor of *T. bisetosa* was reported as a "yeasty or musty smell" (Cavender and Goeden 1982). The odor of *A. mexicana* is likewise yeasty or musty.

Nuptial feeding has not been reported for other *Aciurina* species. Dodson (1987b) reported that adult feeding in general is "negligible" for *A. trixa.* He also noted that no flowers or "obvious exudates" occur on the host plant (*Chrysothamnus nauseosus* [Pallas] Britton) when adults are present. In contrast, flies used in the present study often became so replete with the honey/yeast mixture that ordinary movement, let alone mating, was quite limited. Moreover, stems and leaves of *B. sarothroides* are coated with a sticky material that is attractive to many adult insects (Meyer et al. 1979) and on which adult *A. mexicana* may feed. Adults of *A. ferruginea* also feed (Tauber and Tauber 1967).

Nuptial feeding has been observed (Freidberg 1981 and references therein) or suspected (Cavender and Goeden 1984) for a number of fruit flies. In five species, nuptial gifts consist of an erect, white, frothy mass produced from the mouthparts of males and deposited onto the host plant (Freidberg 1981 and references therein). In two of these species nuptial gifts originate in large, sexually dimorphic salivary glands (Pritchard 1967, Freidberg 1981). In *Spathulina sicula* Rondani, a species with postcopulatory trophallaxis, the salivary glands of males are much larger than those of females (Freidberg 1982 [species as *tristis* (Loew)], Fig. 5). Sexually dimorphic salivary glands also are present in males of *Anastrepha* and *Ceratitis* (Nation 1981), but, at least for *A. suspensa, A. ludens,* and *C. capitata,* nuptial feeding has not been reported (Nation 1972, Pro-

kopy and Hendrichs 1979, Robacker and Hart 1985b). Preliminary examination of the alimentary tract of five male and five female *A. mexicana* showed essentially no intersexual difference in size and shape of the salivary glands. Both sexes possess a relatively large crop.

Unlike the nuptial gifts discussed above, that of *A. mexicana* consisted of drops of a clear fluid. When initially produced it was similar to the fluid in the crops of dissected flies. The amount of fluid produced was greater than would be expected from the salivary glands alone. It seems probable then, that contents of the crop contributed to the nuptial gift of *A. mexicana*.

Mating behavior. — The courtship posture assumed by male *A. mexicana* has not been reported for other *Aciurina* species. The posture is similar to that illustrated for *D. pornia* (Pritchard 1967, fig. 2). An erect posture also has been observed for *Anastrepha ludens* (Robacker and Hart 1985b).

Mounting and copulatory positions of *A. mexicana* were like those described for *A. ferruginea* (Tauber and Tauber 1967). However, once mounted, males did not contact the female's dorsum with their mouth parts as in *A. ferruginea*. Mounting in *A. trixa* is facilitated by the male grasping the female's hindlegs between the tibia and femur of his forelegs (termed "leglock," Dodson [1987a, b]). The forefemora of males are enlarged and males with larger forefemora are more successful in securing copulations (Dodson 1987a). This method of mounting was not seen for *A. mexicana* and subsequent measurements indicated no significant sexual dimorphism in forefemora (Table 1).

Dodson (1987b) reported multiple matings by female *A. trixa*. Females of *A. mexicana* may also be polyandrous. On one occasion a female mated again after 1 d, while on another occasion a female mated again after 1 wk. Conversely, in two trials initiated 2 d after copulation, one female was unresponsive to and the other actively rejected male courtship. Mean duration of copula-

Table 1. Comparison of mean maximum length and width of forefemora among male and female *Aciurina mexicana* (two-tailed *t*-test). Measurements taken with ocular micrometer and dissecting microscope. Means expressed in arbitrary units (35 units = 1 mm).

	$\bar{x}$ (n)	t	df	P
Femur length				
Males	26.9 (11)	0.37	20	>0.25
Females	26.6 (11)			
Femur width				
Males	8.4 (11)	0.93	20	>0.15
Females	8.1 (11)			

tion for *A. trixa* (2.2 h [Dodson 1987b]) was longer than that observed for *A. mexicana* (1.5 h).

Evasive actions taken by female *A. mexicana* to prevent copulation are like those described for *A. ferruginea* (Tauber and Tauber 1967) and *A. trixa* (Dodson 1987b). Females of *Anastrepha suspensa* similarly press their oviscape to the substrate to prevent copulation (Nation 1972).

It is unknown to what extent the mating behaviors observed in the laboratory for *Aciurina mexicana* occur in nature. Observation of behavior in the field was unsuccessful because of low fly densities. However, it is very unlikely that the complex behaviors reported here were laboratory artifacts.

Mating behavior and systematics. — *Aciurina mexicana*, *A. aplopappi* (Coquillett), and *A. thoracica* Curran form Steyskal's (1984) *Aplopappi* species group. Unlike other *Aciurina* species, members of the *Aplopappi* group have host plants other than species of *Chrysothamnus*, and lack surface specializations on the membranous portion of sternum 8 of the ovipositor (Steyskal 1984). The observations reported herein raise the possibility that members of the *Aplopappi* group also have distinctive mating behaviors that further distinguish them from the remainder of the genus.

Eldredge and Cracraft (1980) noted that

"with the exception of the findings of comparative anatomy, no other kind of similarity has been utilized by systematists as much as that of behavior." Current supergeneric classifications of the Tephritidae (e.g. Foote and Steyskal 1987), which are based largely on adult morphology, are problematical. It is now well documented that many fruit flies have characteristic mating behaviors. As shown here, sexual displays are a potentially rich (but unused) source of comparative data. The interspecific distribution of these displays may help resolve or corroborate evolutionary patterns used to construct classifications.

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